A trait-based approach to ocean ecology

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Food-web dynamics under climate change

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Abstract

Climate change affects ecological communities through its impact on the physiological performance of individuals. However, the population dynamic of species well inside their thermal niche is also determined by competitors, prey, and predators, in addition to being influenced by temperature changes. We use a trait-based food-web model to examine how the interplay between the direct physiological effects from temperature and the indirect effects due to changing interactions between populations shapes the ecological consequences of climate change for populations and for entire communities. Our simulations illustrate how isolated communities deteriorate as populations go extinct when the environment moves outside the species' thermal niches. High-trophic level species are most vulnerable, while the ecosystem function of lower trophic levels is less impacted. Open and diverse communities can compensate for the loss of ecosystem function by invasions of new species. Individual populations show complex responses largely uncorrelated with the direct impact of temperature change on physiology. Such complex responses are particularly evident during extinction and invasion events of other species, where climatically well-adapted species may be brought to extinctions by the changed food-web topology. Our results highlight that the impact of climate change on specific populations is largely unpredictable, and apparently well-adapted species may be severely impacted.

Keywords: Population dynamics, Arrhenius, Community ecology

Introduction

Effects of climate change are increasingly observed in the biosphere [1]. The accelerating change prompts the need for assessments of future changes. Ecological communities are particularly vulnerable, but their responses to climate change are also notoriously difficult to predict. Attention so far has focused on predicting the responses of specific populations through the direct impact of changed temperature on their physiology (e.g. [2, 3]) or through bio-climatic envelope and species distribution models [4, 5, 7, 6]. Such models provide credible predictions of species extinctions (and possibly invasions) as the temperature in an area moves outside (or inside) a species' thermal niche. However, populations do not occupy all sites within their thermal niches because they are limited by the interaction with other populations through competition, food availability, and predation. This effect is well known in ecological theory as the difference between the fundamental (thermal) niche and the realised niche [8]. Or, as aptly put by Darwin [9]: "We have reason to believe that species in a state of nature are limited in their ranges by the competition of other organic beings quite as much as, or more than, by adaptation to particular climates".

That climate change impacts cannot be understood solely from physiology is well illustrated by the recent exploration of shifting ranges of fish [10]. While, on average, populations move in the direction of local climate change, there is a large variation in the response of different populations, and some populations even move in the opposite direction of climate change. The large variation clearly indicates that a focus on the physiological impact of temperature is insufficient to predict the direction where a specific population will move under climate change. Consequently, assessing how a future climate may alter existing communities of natural populations requires the integration of at least two effects: the direct impact on the physiology of individuals [2, 11] and the indirect impact on species due to changed species interactions [12, 13]. However, despite the recognised central role of species interactions, they are rarely considered in climate change projections [14].

Assessing the indirect effects due to changed predator-prey relations requires a description of the food-web surrounding a given species. Such descriptions have been developed for simple food-web motifs, such as between a single predator and prey [15, 16, 17] or a three-species food chain

[18]. These studies demonstrate how changes in the prey or predator landscapes may lead to extinctions of specific populations, even for populations that are not themselves directly physiologically impacted by a changing climate. Such indirect effects of climate change might be as important as the direct effects; however, they have not been addressed at the level of entire food-webs in general [20, 13]. Studies attempting to address the entire food-web are limited to specific systems [21, 22], or to using size-based descriptions that do not resolve specific species and extinction events [23, 24, 25]. While these studies illuminate different aspects of the interplay between direct and indirect effects of climate change, a general synthesis has yet to be developed.

What further complicates matters is the invasions of species that are better adapted to the changed environment [26]. On the level of ecosystem function, invasions might be able to compensate for the loss of function due to extinctions. Theoretically, however, dealing with invasions is even harder than dealing with extinctions because it requires an understanding of where an invading species fits into an existing food-web. Such a description is not possible with the common approach to food-web models, where the topology of the food-web is assembled from observed feeding links [21] or statistical rules [27, 28]. Dealing with invading species requires a trait-based approach which describes the food-web relations through a few relevant traits [29]. Only with a trait-based approach can we include the effects of invasions and obtain a general description of changes in ecosystem function.

Here we use a general food-web model as a test-bed for exploring the impact of climate change on a community: how climate change leads to extinctions and invasions, and ultimately to changes in ecosystem function. The model belongs to an established class of food-web models built upon size-based description of predator-prey interactions [30] that have been shown to replicate the general structure of food-webs [31, 32], and have been successfully applied to predict population dynamics and consequences of species extinctions [33, 34, 35, 36]. Our version of the food-web model is augmented with a trait-based description of species interactions, which makes it able to handle invasions [37]. We use the model to explore the relative the importance of direct vs. indirect effects of climate change. Specifically, we address three questions: (1) How does climate

change affect isolated systems that are closed towards species invasions vs. systems that are open towards species invasions? We expect that isolated systems lose functions and resilience, while invasions might be able to offset losses in functions in open systems. (2) What is the main driver of extinction: is it the direct physiological effects on the individuals, or is it the indirect effect of changes in feeding interactions in the food-web? (3) How important are cascading effects, i.e., do extinctions or invasions lead to secondary extinctions or invasions? We use simple food-web metrics to measure changes in function and resilience: changes to ecosystem function are measured by species richness, the maximum trophic level, the size-spectrum exponent (i.e., the exponent b in the abundance-mass scaling, that is, abundance $\propto$ mass^b), and the primary production transferred to higher trophic levels. A change in resilience towards future changes is indicated by the Community Temperature Index (a measure of the average temperature of the species' thermal niche; [38]). Impacts of climate change on specific populations are measured by changes in birth rate and population biomass.

Methods

Our food-web model follows a standard Lotka-Volterra interaction between predators and prey. In the following we show the main equations and a detailed model description is presented in the *SI*.

The rate of change of biomass B_i of population i is given by:

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = \left[\alpha\rho(T_{\mathrm{env}} - T_{\mathrm{mid}.i})(E_{\mathrm{res}.i} + \sum_j \theta_{j,i}B_j) - M_i - \sum_j \theta_{i,j}B_j\right] B_i.$$

The first term on the right-hand side represents gain of energy (mass per time) from consumption of the basal resource (i.e., $E_{\mathrm{res}.i}B_i$) and from predation on smaller consumer species (i.e., $\sum_j \theta_{j,i}B_jB_i$). The second term (i.e., M_iB_i) is the mass specific loss due to metabolic costs and other mortality than predation. The last term (i.e., $\sum_j \theta_{i,j}B_jB_i$) is losses to predation by larger consumer species. α is the assimilation efficiency and $\theta_{j,i}$ is the preference of species i for preying on species j. All rates (feeding and metabolism: $\theta_{i,j}$ and M_i) are scaled with body size of the species [39] and with envi-

ronmental temperature T_{env} according to an Arrhenius relationship [40]. The term $\rho(T_{\mathrm{env}} - T_{\mathrm{mid}.i})$ represents the thermal niche of the species, where $\rho(T) = 1 - u^{T-T_{\mathrm{scope}}/2} - u^{-T-T_{\mathrm{scope}}/2}$. It is a non-negative function with the value one in a range of ± 5°C (i.e., $T_{\mathrm{scope}}/2$) around the midpoint of the species' thermal niche $T_{\mathrm{mid}.i}$ and the value drops down quickly towards zero when environmental temperature goes outside of the thermal niche (Fig. S1). In nature, increased temperature also results in reduced body sizes [12, 41]. Since this effect affects all species similarly it is not expected to impact predator-prey or competitive relationships significantly, and in the interest of maintaining a simple model we do not resolve this effect.

Interactions between species are determined by body size w_i and habitat trait x_i, which in combination form the interaction coefficient $\theta_{j,i}$: large species eat smaller species [42, 30] within the same habitat. This procedure combines size-based predator-prey interactions with classic competition theory [43] to determine interactions between populations by their body size and habitat trait [44]. The resource biomass grows dynamically and the loss of resource biomass is solely owing to the predation of all consumer species.

Food-webs are assembled from pools of species with randomly assigned traits of body size, habitat, and midpoint of thermal niche (detailed numerical implementation is presented in *SI*). The assembly process allows new species from the pool to invade sequentially until the food-web reaches a closed state where no species from the pool can invade (Fig. S2) [45, 46] at a constant environmental temperature (i.e., 10°C). Species in the pool have a range of midpoint temperatures from 4-20°C, however, only species with a temperature close to the environmental temperature will be able to invade the community. From the closed state, the temperature is increased in 0.05°C steps. Invasions from species in the pool are allowed in each step for open communities but not for isolated communities.

Five macroecological metrics of ecosystem function are calculated. The species richness is simply the number of persistent species in the community, and it measures the general resilience of the community towards change. The maximum trophic level, the size-spectrum exponent, and the primary production transferred to higher trophic levels measures the degree to which the energetic

potential of the community is realized. A fully realized community is expected to have 6 trophic levels [37], a size-spectrum exponent of -1.05 for the chosen parameters [37], and high primary production. Deviations from these expectations, lower maximum trophic level, or more negative exponent, indicates a community that is out of equilibrium, i.e., where the diversity is insufficient for the community to realize the full energetic potential of the primary production. The trophic level is fractional and calculated as the average trophic level of the prey of the focal species plus 1 [47]. The size-spectrum exponent measures the power-law exponent fit to the biomass distribution function, estimated using the generalized cumulative distribution function [48]. The primary production is defined as the averaged utilization of resource biomass relative to the carrying capacity (see Numerical Implementation in *SI*). Finally, the Community Temperature Index is calculated as the mean midpoint of the thermal niches of the species in the community. The difference between the Community Temperature Index and the environmental temperature measures the degree to which the community is balanced with respect to the environment – a community with a dominance of cold-adapted species relative to the environmental temperature will have a lower resilience towards future climate change, than a community with an equal ratio species which are cold- and warm-adapted relative to the current environment. The impacts of climate change on individual populations in the food-web are measured by changes in their birth rates (the first term on the right-hand-side of Eq. 1), and by changes in their biomass.

Results

Fig. 1a shows an example of a community assembled by successive invasions. A small change in temperature has little effect, but when the temperature changes above a threshold, a species becomes extinct. This extinction leads to a re-wiring of the food-web (Fig. 1b). The re-wiring opens up niches for invasions, which again may induce secondary extinctions (Fig. 1c). Note, that the two extinctions triggered by the invasion were of warm-adapted species, for which the direct effects of climate change are small or even positive. Such extinction and invasion cascades illustrate

how the impact of climate change on one species radiates through the food-web to profoundly affect apparently climatically well-adapted species.

Impact on ecosystem function and resilience

Extinctions or invasions in a specific food-web are dramatic events that may trigger secondary extinctions, with concomitant loss of function and deterioration of community metrics (thin lines in Fig. 2). However, when many realizations of food-webs are averaged, or over longer time periods, the average ecosystem function is less variable (thick lines in Fig. 2).

Changes in community metrics show some deterioration of the community as the temperature is increased (Fig. 2). In isolated communities, the diversity diminishes as species become extinct (Fig. 2a). In open communities, invasions of new species compensate for some of the loss, though not fully. As a consequence, the community function declines: maximum trophic level declines and the size-spectrum exponent becomes steeper (Fig. 2b,c). The decline of the maximum trophic levels shows that the largest species at the top of the food-web are the first to be lost, as the establishment of top predators is conditioned on the trophic levels below them being functionally intact. The loss of the top predators is the driver behind the steepening of the size-spectrum. Again, for these two metrics, invasions in open communities compensate for the losses in function experienced by the isolated communities, to the degree that overall function is only weakly affected. The amount of primary production utilized by the community is not much affected, not even in the isolated communities (Fig. 2d). The primary production is used by the lowest trophic levels in the food-web, and as these species are not conditioned on the presence of other species, they are less affected, and their function is therefore almost intact. Finally, as the environment warms, the Community Temperature Index falls out of step with the environmental temperature (Fig. 2e). Consequently, the species in the food-web become increasingly cold-adapted relative to the environment, and the food-web loses the resilience to further temperature changes. By and large, the functions of isolated communities begin to deteriorate once the change in temperature exceeds 1 °C as species goes extinct, while the invasions that occur in the open communities are able to compensate for

most of the lost function.

The functional metrics change less for systems with high diversity than for those with low diversity (Fig. 3). Thus, species diversity increases the resilience of the community in the face of climate change. Communities with more than thirty species experience little change in function when the temperature changes, while less diverse communities lose more function. The most resilient functions are the maximum trophic level and the size-spectrum exponent, while the primary production is surprisingly most sensitive to climate change, which might be due to the amplification of the short-time absolute changes during averaging.

We explore the importance of direct vs. indirect effects of climate change by looking at why species go extinct (Fig. 4). Extinctions of species close to their thermal niche limit are due to the direct effect of a change in temperature, while extinctions of species that are well-adapted, i.e., far from their thermal limits, must be due to the re-organisation of the food-web, i.e., an indirect effect. By far the largest fraction of extinctions happens when the environmental temperature is well within species thermal niche. This result indicates that the indirect effects of climate change due to food-web re-organisation are much more important than the direct physiological effects of climate change on specific species. These indirect effects happen due to the cascading effects of those extinctions that occur due to the direct effects of climate change. Again, whether a community is isolated or open is important, with isolated communities being driven to a higher degree by extinctions that are directly triggered by the physiological effects of climate change.

Impact on populations

The relative importance of direct and indirect effects of climate change is evident in the change of birth rates and biomass of individual populations (Fig. 5). The birth rate (Fig. 5a) is generally increasing in response to increased temperature, until the point where the environmental temperature goes beyond the species' thermal niche. That pattern is to be expected as a direct response to how individual physiology responds to warming. However, many populations show strong deviations from this pattern of slowly increasing birth rates with temperature. The deviation from the

average is amplified in the population biomass, where no distinct pattern between species emerges – biomass may increase or decrease as temperature changes, largely independent of whether the species are warm- or cold-adapted relative to the environmental temperature (Fig. 5b). Cold-adapted species are more likely to have negative changes than warm-adapted species as they are prone to go extinct, but overall warm- and cold-adapted species have similar responses (Fig. 5c). Consequently, the effects of climate change on any specific population cannot be predicted without accounting for species interactions. The only exception is species close to their thermal limits which are forced to extinction.

Discussion

Taken together, our model simulations demonstrate how an understanding of physiology is insufficient to predict population responses to climate change. Changes in population biomasses are determined by the changes in the food-web to a much higher degree than by the species' physiology (Fig. 5). The implications go beyond changes in population biomasses as even extinctions are predominantly driven by other reasons than physiology (Fig. 4). Thus, complex interactions between species play a major role in predicting climatic response of individual species. The dominance of indirect effects does not make direct effects of climate change on physiology unimportant, including species range shift towards higher latitude and altitude [49], phenology shift [50], and reduced body size [12, 41]. However, it does imply that while climate envelope models [4, 5, 6] correctly predict extinctions of species at the end of their climate range, they fail to predict the effects of climate change on species well inside their thermal niche.

The impact of climate change on community function and resilience depends on whether invasions of new species are able to compensate for the loss of function that occur through extinctions. In isolated communities, species richness declines and the communities become unable to support higher trophic level species, in accordance with mesocosm experiments [51]. In contrast, communities that are open to invasions are able to adapt to climate change. Marine pelagic ecosystems

are good examples of very open systems, where planktonic species are transported far via ocean currents or ship ballast water [52], and fish can swim long distances. Indeed, marine communities have shown a correspondence between the change in sea temperature and the Community Temperature Index [38, 53], which indicates that invasions of new species and a high species diversity buffer against the effects of climate change [51]. An exception is tropical oceans where there are no warm-adapted species to invade [38, 53] (Fig. S6). In such places, and isolated ecosystems, maintaining ecosystem structure and function requires evolutionary adaptation [54, 55]. Terrestrial systems are expected to be more isolated than marine systems, with oceanic island as the extreme example. However, even on the continents, dispersal is limited by geographical barriers, or by lower connectivity [56] of increasingly fragmented agricultural landscapes [57].

The model is deliberately kept simple in order to obtain general insights into how species interactions affect community responses to climate change. Importantly, the model allows invasion of new species into a community. While our model captures the salient features of how predator-prey interactions and exploitative competition interact to shape community structure and set the stage for dynamics of individual populations, the simplicity of the model means that other aspects are not resolved. For instance, we assumed that the rate of warming is slow relative to the life-span of the species. With the present pace of warming this may be incorrect for the largest and longest-lived species. As these species are the ones most sensitive to the indirect effects of warming, a faster pace of climate change will make them even more vulnerable. We further assumed that modelled species all have the same width of thermal niche, symmetric around the midpoint, which is a simplification. Experimental studies show that the width of thermal niche varies between species [2, 41] and is asymmetric around the midpoint temperature. The asymmetry will shift the optimum of the temperature niche towards a higher temperature than the midpoint temperature used here. This shift will, on average, mean that species are closer to their upper temperature limit, and they are therefore more likely to go locally extinct due to the direct effect of climate change than represented in the model. Nevertheless, this effect is relatively small and not likely to overrule the strong effect of most extinctions being driven by indirect effects. Incorporating asymmetric temperature niches

might increase realism, but as long as species go extinct once environmental temperature exceeds the species' thermal limits, the general conclusion remains valid: understanding changes in species interaction is indispensable for predicting the responses of ecological communities to global warming. A sensitivity analysis with asymmetric thermal niche (Fig. S3) displayed only limited difference between the simulations with symmetric thermal niche (Fig. S4). Besides this model variant, our results are also robust for other variants including different approaches of invader selection such as selecting an invader with a midpoint temperature closest to the environmental temperature or with the highest fitness (Fig. S5), and smaller variance in temperature trait without skewedness towards either cold- or warm-adapted species. Finally, sensitivity tests also show that the model is not sensitive to changes in the value of the preferred predator-prey mass ratio (Fig. S7). Taken together, the model results appear to be fairly robust.

We explored maybe the most common way in which species interactions could affect the climatic responses of population and communities, namely by gain and loss of feeding links due to extinctions or invasions. Obviously, to fully assess food-web responses to climate change, future studies may have to simultaneously consider other biotic factors such as behaviour change, variation within populations, and evolutionary adaptation in a food-web context. Integrating all these processes convincingly in a general model framework remains a future challenge. A potential helpful approach is the stochastic individual based food-web models that can simultaneously incorporate a variety of individual traits and where community properties emerge from decision-making individuals [58, 59]. In conclusion, climate-induced indirect effects such as secondary extinction are stronger than the direct physiological effects on individual species. Diversity buffers against the effects of climate change, in particular if warm-adapted species are able to invade. Improving predictions of the effects of climate change on biodiversity requires increased knowledge of species interactions [14].

Data accessibility

This article has no additional data.

Ethics statement

This article does not involve work on human subjects or animals.

Competing interests

We have no competing interests.

Author contributions

K.H.A. designed the study and, together with L.Z. and M.H., developed the model. L.Z. performed numerical simulations and data analysis, and wrote, together with K.H.A., the manuscript draft. All authors contributed to discussion of results and the final text.

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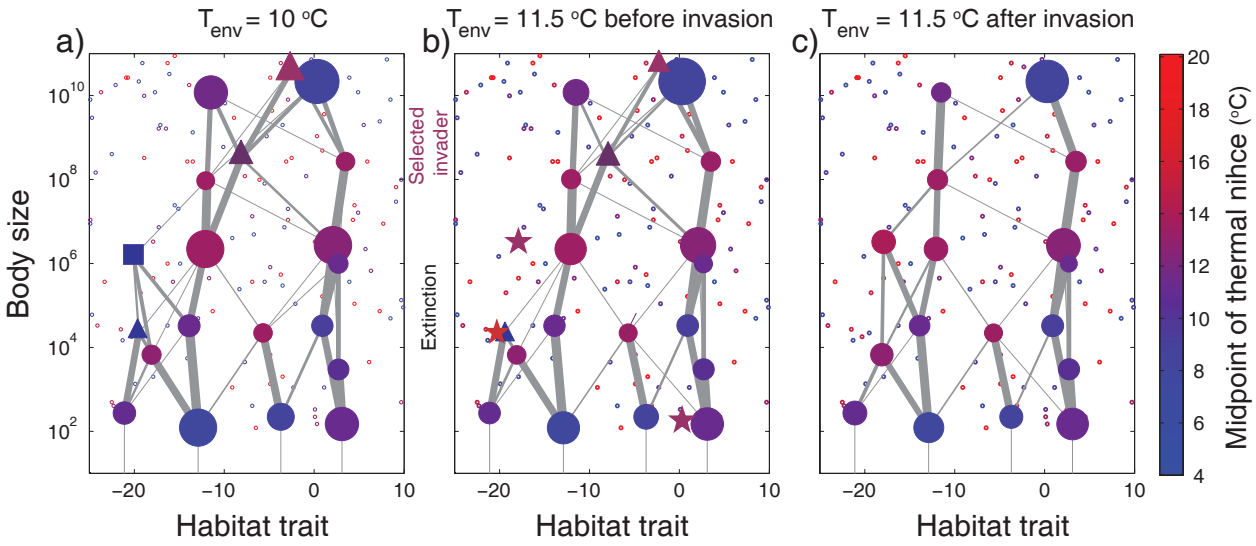

Figure 1: Example of how increased temperature impacts a simulated food-web. Small open circles indicate the species in the species pool of size 200. The position of each population is determined by body size (y-axis), habitat trait (x-axis), and the colour denotes the midpoint of the thermal niche. Solid symbols connected by lines indicate the species in the food-web with the area of the symbol being proportional to population biomass and line width to interaction strength. a) Food-web assembled under constant temperature ($T_{\mathrm{env}} = 10°\mathrm{C}$). This food-web community has achieved a structure where none of the species from the pool can invade. b) After increasing the temperature to 11.5°C, one species goes extinct (square) and the food-web is changed in both topology and population biomass. The change re-opens the community to invasion and three species (stars) are able to invade. c) After introducing one of them (middle star), the invader establishes itself and rewires the food-web topology by inducing one extinction through predation (bottom triangle) and two secondary extinctions (top two triangles).

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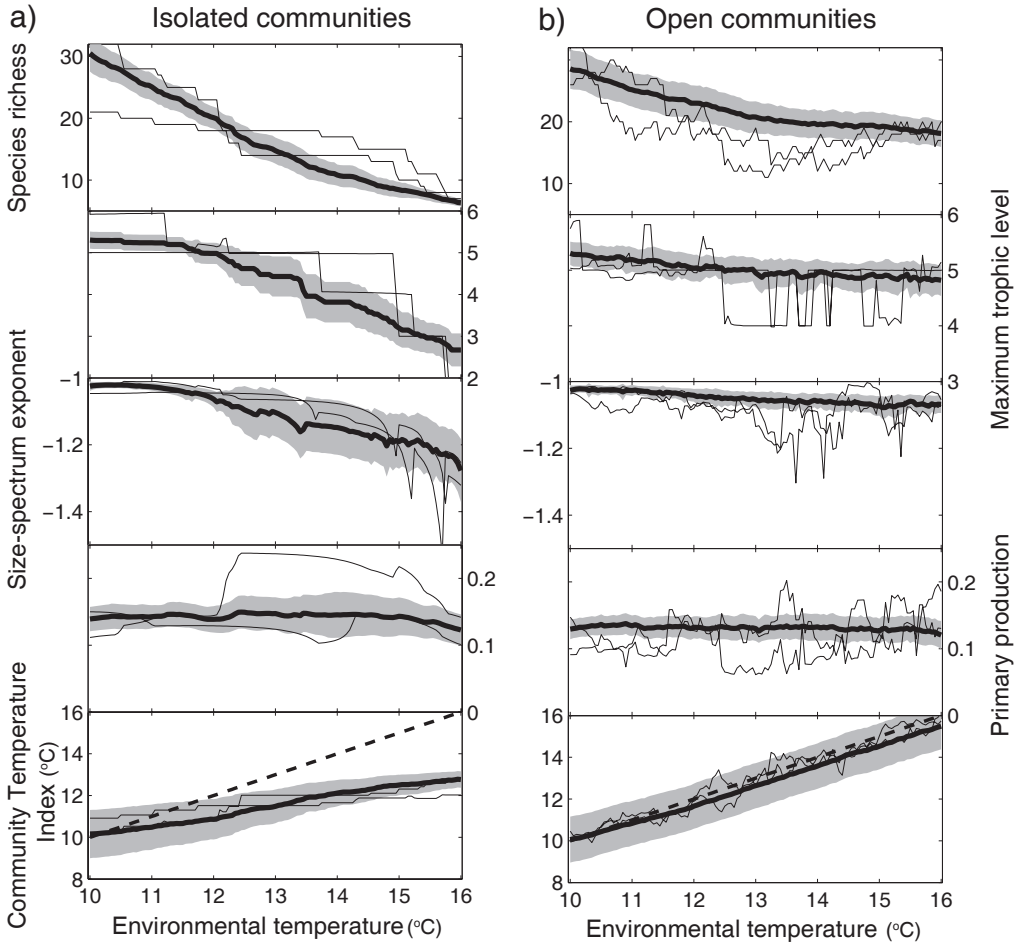

Figure 2: Change in community-level metrics under climate change (from top to bottom; see Methods for description): species richness, maximum trophic level, size-spectrum exponent, primary production transferred to higher trophic levels, and the Community Temperature Index compared to the environmental temperature (dashed lines). a) Isolated communities where only extinctions occur. b) Open communities where invasions from the species pool are allowed. Thin lines represent two randomly sampled communities and the thick lines represent the community average over 100 replicates (for pool size of 400) with the shaded areas representing the standard deviation.

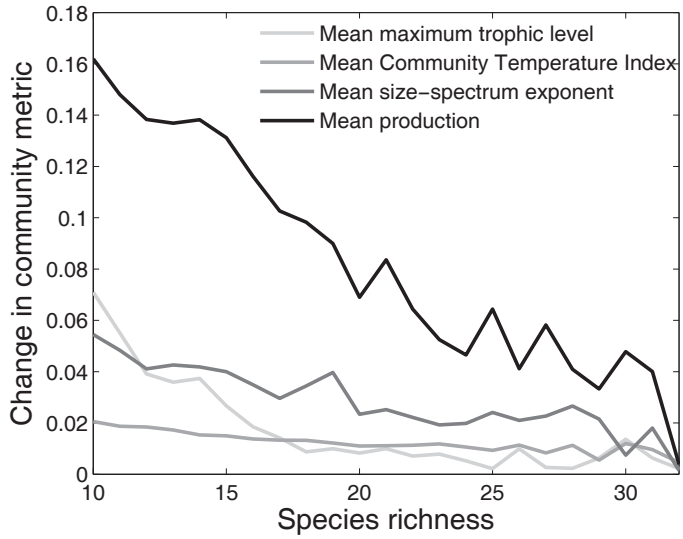

Figure 3: Averaged absolute change in community-level metrics for open communities with varying species richness following a 0.05°C change in temperature across all replicates regardless of pool size (i.e., 100, 200, 400, 800). For each replicate, community metrics at different environmental temperature are scaled with their respective community metrics at previous temperature step.

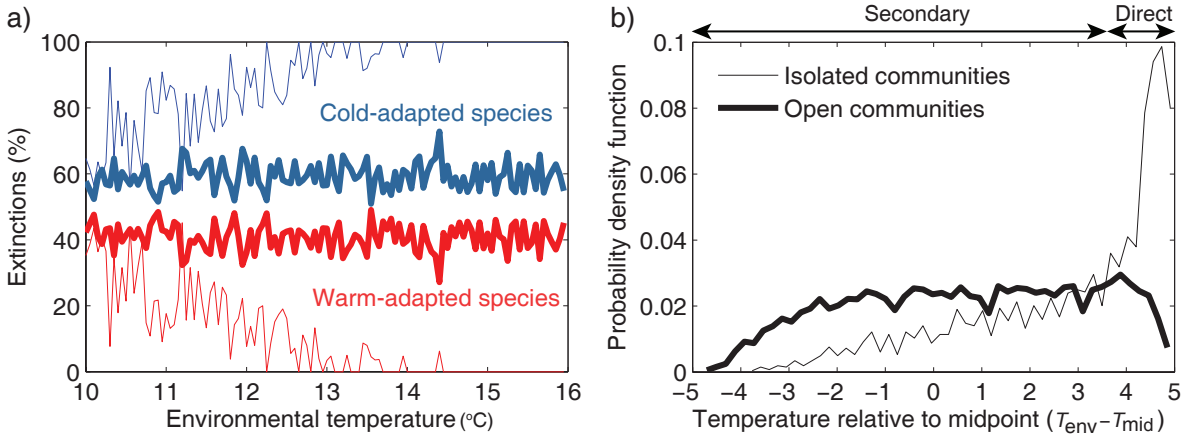

Figure 4: Extinctions of cold-adapted (blue) vs. warm-adapted species (red) in isolated (thin lines) and open communities (thick lines). a) The development of extinction as the temperature is increased from 10°C. b) Probability density function of temperature difference between environmental temperature (T_{env}) at which species go extinct and the middle point of species? midpoint of thermal niche (T_{mid}). Extinction events are interpreted as being triggered by the direct physiological impact if the temperature difference is greater than ≈ 3.5°C; all other extinction events are due to changes in species interactions, i.e., secondary extinctions. Averages are across all replicates associated with pool size of 400.

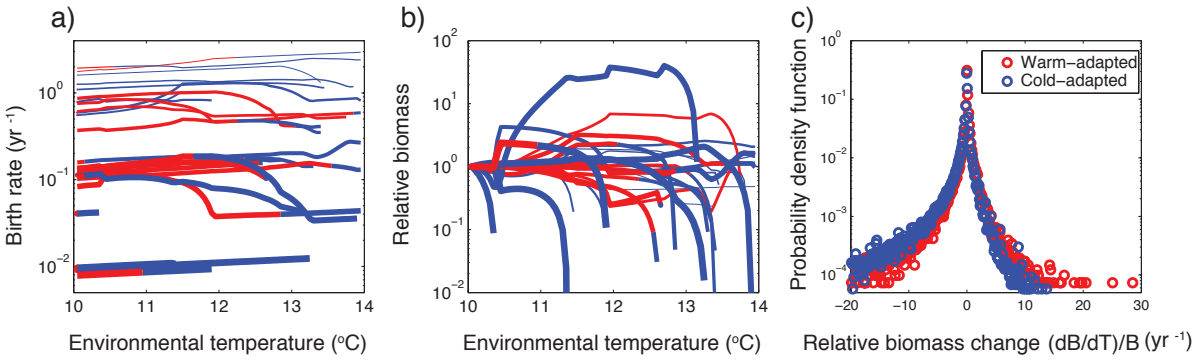

Figure 5: Change in population birth rate (a) and biomass (b) under a climate change scenario for a given community of initially 25 species at $T_{\mathrm{env}} = 10°\mathrm{C}$, and (c) the probability density function of the change in biomass of a species following a 0.05 degree change in temperature (across all replicates for pool size of 400). Line thickness increases in proportion to log body-size. Line colour indicates whether the species are relatively warm- or cold-adapted (red vs. blue). No invasions are allowed.